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A null-model analysis of the spatio-temporal distribution of earthworm species assemblages in Colombian grasslands

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Abstract: Earthworm assemblages are usually spatio-temporally structured in mosaics of patches with different species composition. We re-analysed results of past research carried out in Eastern Colombia to explore how interspecific competition accounts for this pattern. In three sown pastures and three native savannas, density data matrices were obtained from spatially explicit samplings at several successive dates, and spatio-temporal patterns of species assemblages were described through partial triadic analyses and geostatistics. This first analysis detected assemblage patchiness in the six plots at spatial scales ranging from 6 to 33 m. Species richness ranged from 5 to 6 species per plot. Null models were further used to analyse niche overlap and morphometric distribution patterns at two different scales, i.e. at the 'plot level' and the 'patch level'. Seasonal and vertical niche overlaps were higher than expected by chance at both scales, indicating high environmental constraints on assemblage membership. Within-patch overlaps were lower than plot-scale overlaps. Biometric niche overlap was random at the plot level and was weakly lower than that expected by chance in patches. Body weight was significantly overdispersed and constant whatever the scale, while body length and diameter showed a similar trend within patches. These results suggest that earthworms form distinct assemblages within patches, mainly driven by deterministic responses to competition: ecologically similar species avoid competition through spatial segregation, whereas a minimal level of ecological segregation is required to allow co-existence in a given patch.

Key Words: community ecology, interspecific competition, niche overlap analysis, scale dependence, size distribution analysis

INTRODUCTION

The study of the spatial pattern of soil biota and the factors by which they are governed is a key research area in understanding the structure and function of soil biodiversity and their relationships with above-ground processes (Ettema & Wardle 2002, Ettema *et al.* 2000). To date however, soil communities have been minimally considered in spatial ecology when compared with above-ground biota (Ettema & Wardle 2002). As an example, despite the early recognition of the fundamental role played by earthworms in soil processes (Darwin 1881), the very first descriptions of their spatial distribution were published as late as the 1950s (Boyd 1957, Guild 1951). Earthworm spatial patterns are however likely to contribute to existing heterogeneity in soil resources and microhabitats, and to promote species co-existence through greater resource partitioning (Lavelle 1996, 2002; Wardle 2002). In this sense earthworms could be keystone organisms in soil faunal communities (Lavelle *et al.* 2006).

In recent studies, spatial statistics have been used to describe the horizontal spatial patterning of earthworm assemblages at local scales (i.e. habitat surfaces of about 1 ha). In most cases, species are aggregated in patches over ranges of 20–50 m, each of them characterized by a dominant species assemblage that seems to be temporally stable for about 20 mo (Decaëns & Rossi 2001, Hernández *et al.* 2007, Jiménez *et al.* 2001, 2006a; Margerie *et al.* 2001, Nuutinen *et al.* 1998, Rossi 2003, Rossi & Lavelle 1998). The determinants of these patterns are hardly identified as they probably imply both environmental and population or community factors operating and interacting at different scales (Barot *et al.* 2007). For instance, species-assemblage patchiness may result from

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species responses to the heterogeneity in plant cover and soil properties (Margerie *et al.* 2001, Phillipson *et al.* 1976, Poier & Richter 1992), intrinsic population processes such as reproduction rates and limited dispersal (Barot *et al.* 2007, Jiménez *et al.* 2001, Rossi *et al.* 1997, Whalen & Costa 2003), or interspecific competition leading to spatial segregation between species pairs with high niche overlap (Jiménez & Rossi 2006, Jiménez *et al.* 2006a).

The implication of interspecific interactions, in particular competition, in shaping the structure of natural communities has been reported for many animals and plants (Connell 1983, Diamond 1975, Goldberg & Barton 1992, Gotelli & McCabe 2002, Schoener 1974, Wilson & Habiba 1995). According to the theoretical framework of interspecific competition, two basic predictions may be formulated (Gotelli & Ellison 2002): first, among a set of communities or species assemblages, species should co-occur less often than expected by chance (EBC) (Diamond 1975, Pielou & Pielou 1968); second, within a community or species assemblage, co-existing species should present a lower niche overlap than EBC (Schoener 1974). Classic examples of the latter include limitation of similarity in body size or in multi-trait morphology (Hutchinson 1959, MacArthur & Levins 1967, Weiher & Keddy 1995, Weiher *et al.* 1998). Non-randomness in niche overlap and co-occurrence patterns is thus considered to reflect competition constraints on community assembly. Recently, null model analysis has emerged as an efficient tool to identify non-random community patterns (Gotelli 2001, Gotelli & Graves 1996). They are pattern-generating models that deliberately exclude a mechanism of interest (for instance competition), and allow testing of observed data against randomized null communities (Gotelli 2001, Gotelli & Graves 1996). They were successfully used to highlight and interpret, among others, non-random patterns in body-size distribution (Feeley 2003, Gotelli & Ellison 2002) and niche overlap (Albrecht & Gotelli 2001, Hofer *et al.* 2004) in different animal assemblages.

In this paper, we re-analysed with null models the data collected in the course of different studies of the spatio-temporal distribution of earthworm assemblages in Colombian tropical grasslands (Decaëns 1999, Decaëns & Rossi 2001, Jiménez 1999, Jiménez *et al.* 2006a). All these studies described a consistent horizontal patterning in alternated patches dominated by particular species assemblages. We hypothesized that these patches result from predictable assembly rules related to interspecific competition, i.e. are a consequence of spatial exclusion among competing species. If so, segregation should be most evident, based on the degree of niche overlap, at local scales ('patch-level assemblages', i.e. the list of dominant species characterizing a given patch), and less so at larger scales ('plot-level assemblages', i.e. the list of species present in a given grassland plot). We thus expected to observe two types of non-random patterns: (1) within-patch niche overlap should be lower than EBC and lower than plot-scale overlap (MacArthur & Levins 1967, Weiher & Keddy 1995); (2) morphometric distance (size ratio) between species co-existing in a given patch should be higher and more constant than EBC, and higher and more constant than at the plot level (Brown & Wilson 1956, Dayan & Simberloff 2005, Gotelli & Ellison 2002, Hutchinson 1959). We tested this hypothesis for different dimensions of the niche (seasonal activity, vertical distribution and multi-trait morphology) and by separately analysing different biometric traits.

An alternate hypothesis is that patchiness reflects environmental heterogeneity and that patch-level assemblages are composed of species sharing the adapted traits to the patch environment. In this case, dominating species of a given patch should present a higher niche overlap than EBC and than at the plot-scale (Keddy 1992, Weiher & Keddy 1995). Morphometric distance within a given patch should also be lower and less constant than EBC and lower and less constant than for plot-level assemblages.

STUDY SITE

A data set was compiled from two studies carried out at the CIAT-CORPOICA Carimagua Research Station, in the phytogeographic unit of the well-drained isohyperthermic savannas of eastern Colombia (4°37′N, 71°19′W, 175 m asl). Climate is subhumid tropical with a mean annual rainfall and temperature of 2280 mm and 26 °C, respectively (1972–1995, CIAT data). Study plots were located in an upland area with a well-drained silty clay Oxisol (Tropeptic Haplustox Isohyperthermic; USDA classification), characterized by its acidity ($pH[H_2O] = 4.5$), a high Al saturation (>80%) and low values of exchangeable cations. All the study plots were located in the same area of the Research Station, with no more than 100 m between each other.

Sampling was carried out in three savanna plots and three sown pastures. Savanna plots (Savanna 1 to 3) were all devoid of any management, and had areas of 0.36 (Savanna 2 and 3) and 2.26 ha (Savanna 1). Vegetation was dominated by the Poaceae *Andropogon bicornis* L., *Gymnopogon foliosus* (Wild.) Nees, *Panicum* sp., *Trachypogon* sp. and *Imperata brasiliensis* Trin. Pasture 1 was a 1 ha and 18-y-old plot of *Urochloa decumbens* (Stapf) R.D. Webster (Poaceae) and *Pueraria phaseoloides* Benth. (Fabaceae), grazed by cattle at an average stocking rate of 1.75 Animal Unit (AU) ha^{-1} (1 AU = 250 kg). Pasture 2 was a 0.72 ha and 3-y-old plot of *Urochloa humidicola* (Rendle) Morrone & Zuloaga (Poaceae), *Arachis pintoi* Krap. & Greg (Fabaceae), *Stylosanthes capitata* Vog. (Fabaceae) and *Centrosema acutifolium* Benth. 'Vichada'

(Fabaceae), grazed by cattle at an average stocking rate of 2 AU ha^{-1}. Pasture 3 was a 0.72 ha and 1-y-old plot of *Panicum maximum* and *A. pintoi*, managed similarly to pasture 2.

METHODS

Earthworm sampling

In each plot, samples were taken on a regular grid of evenly spaced points. The dimension of the grids varied depending on plot size: 8 × 8 sampling points each 10 m in Pasture 1 and Savanna 1; 8 × 15 points each 5 m in Pastures 2 and 3; 4 × 15 points each 5 m in Savanna 2 and 3. Each plot was surveyed at different successive dates: November 1993, 1994 and May 1995 for Savanna 1; September 1993, October 1994 and June 1995 for Pasture 1; and every 2 mo from October 1995 to August 1997, with exception of December 1995 and July 1997, in the other plots. Thus, the total study period for each plot ranged from 21 to 22 mo.

At each point, a soil monolith of 40 × 40 cm (Savanna 1 and Pasture 1) or 25 × 25 cm (other plots) was dug out down to 30-cm depth and hand sorted in the field. Collected earthworms were identified, counted and replaced in the monolith point with the sorted soil. Prior to the monolith extraction, the density of the large species *Martiodrilus* sp. was estimated by counting its fresh casts at the surface of a 1-m^2 square that was centred on the monolith (Jiménez *et al.* 1998a). Soil monoliths at subsequent dates were taken in points separated about 30–50 cm from the sample of the first date. This displacement in space was considered negligible at the scale of the plot, and sampling coordinates were taken as identical from one date to another.

As the characteristics of samples varied significantly among plots, we used non-parametric regression (using Ecosim software, Acquired Intelligence Inc. & Kesey-Bear, http://garyentsminger.com/ecosim.htm) to verify that differences in observed patterns were not a by-product of different sampling procedures. This procedure was run to test the effect of sampling grid size, distance between sampling points, sample sizes and sampling frequency (dependent variables) on patch spatial range (independent variable). Non-parametric regression fits a standard linear regression to the data set, and then uses randomization to test the null hypothesis that the slope, intercept or correlation coefficient equals 0. In all cases, slope, intercept and correlation coefficient were as EBC ($r^2 = 0.00$; $P = 0.457$ for grid size, $r^2 = 0.58$; $P = 0.129$ for distance effects, $r^2 = 0.58$; $P = 0.140$ for sample size, $r^2 = 0.58$; $P = 0.147$ for sampling frequency). The different sampling designs were thus assumed to address processes at similar spatial scales.

For niche overlap calculations, we used the data sets obtained by Jiménez (1999) from a stratified random sampling performed from April 1994 to September 1995 in the Savanna 1 and Pasture 1. In each plot, five monthly 1-m^2 monoliths were dug out down to 50 cm and hand sorted in 10-cm increment layers. Two 20 × 20 × 20-cm soil cores were sampled 1 m distance from the monolith; the soil was then washed and sieved to collect small species that were not efficiently collected by hand sorting (Jiménez *et al.* 2006b). Earthworms were fixed and stored in 4% formaldehyde, identified and counted in the laboratory to calculate mean population density for each sampling month and in each soil layer. Body length (mm), weight (g) and preclitellar diameter (mm) were measured on fixed specimens for all specimens that were complete. Voucher specimens of all species were deposited in the Universidad Tecnologica de Pereira (Colombia). For both the grassland and the savanna, we obtained three matrices describing species according to their temporal dynamics over a complete seasonal cycle (July 1994–June 1995), vertical distribution and biometric traits.

Partial triadic analyses and identification of patch-level assemblages

The partial triadic analysis (PTA) is used to analyse a chronological series of tables that describes the same objects with the same variables (Kroonenberg 1989, Rossi 2003, Thioulouse & Chessel 1987). It allows extraction of the multivariate structure that is expressed through the different dates, and describes dominant patterns in its first axes while relegating the random noise to further axes that are not retained for interpretation (Rossi 2003). For each plot, we used t matrices (t = number of sampling dates), each one describing n observations (sampling points) for p variables (species abundances). Each PTA consisted of two successive steps: (1) The interstructure analysis provided a global description of the sampling points as a function of the typology of the sampling dates. For each species and in each plot, spatial patterns that were stable over the study period were described by mapping the coordinates of the sampling points on the first interstructure axis on the sample grid. (2) The compromise analysis provided a description of sampling points as a function of the species typology. It was used for each plot to identify the species assemblages that characterized similar patches at different dates, to which we refer herein as the 'patch-level assemblages'. On the first compromise axis, a patch-level assemblage was defined as a group of species displaying coordinates of the same sign. The maps of the coordinates of the sampling points on the first compromise axis thus described the spatio-temporal distribution of these patch-level assemblages.

All the computations and figures were processed with the module STATIS and other graphical modules of the software ADE-4 (Thioulouse *et al.* 1997).

Moran's autocorrelogram

For each PTA, we tested the presence of spatial autocorrelation in species assemblages using Moran's correlograms (Legendre & Fortin 1989, Sokal & Oden 1978) computed with the sample scores on the first compromise axis (Decaëns & Rossi 2001). The correlogram shows the changes of autocorrelation coefficients with increasing distance. It thus indicates the spatial range of the observed spatial patterns and provides a test of the significance for non-randomness (Sokal & Oden 1978). Data were allocated to nine (Pasture 1 and Savanna 1), 12 (Savannas 2 and 3) or 14 (Pasture 2 and 3) distance classes depending on the size of the analysed matrix. Moran's index was calculated using the 'Autocorrélation 3.03' module of the 'R Package' (Université de Montréal, Canada), and the normality of the data distribution was tested with a Kolmogorov–Smirnov test before computation with the 'VerNorm 3.0' module of the same software. When necessary, the Box-Cox transformation was used to reduce the asymmetry of the frequency distribution (Sokal & Rohlf 1995).

Temporal and vertical niche overlap analysis

Niche overlap analysis was undertaken for the six plot-level assemblages and the twelve patch-level assemblages identified by the compromise analyses. For each of them, we built an individual matrix in which rows and columns represented species and niche categories, respectively, and we tested if niche overlap significantly differed from the corresponding value under the null hypothesis (i.e. random assemblage). We used Pianka's index (Pianka 1973) and the Czechanowski index (Feinsinger *et al.* 1981). For species j and k, with resource utilizations p_{ji} and p_{ki}, Pianka's overlap index of species j on species k (O_{jk}) is given by the following formula:

$$O_{jk} = O_{kj} = \frac{\sum_{i=1}^{n} p_{ji}\, p_{ki}}{\sqrt{\sum_{i=1}^{n} \left(p_{ji}^2\right)\left(p_{ki}^2\right)}}$$

For species j and k, with resource utilizations p_{ji} and p_{ki}, Czechanowski overlap index (O_{jk}) is:

$$O_{jk} = O_{kj} = 1.0 - 0.5 \times \sum_{i=1}^{n} |p_{ji} - p_{ki}|$$

The level of niche breadth was calculated with both indices for three distinct dimensions of resource utilization. (1) Although temporal partitioning may be relatively uncommon in animal communities (Schoener 1974), several examples involving invertebrates have been described to date (Gotelli & Graves 1996). We considered that time was of potential importance for earthworm assemblages because the high seasonal fluctuations of important resources, such as water and litter, may cause diet shifts according to the time of the year. For this analysis, we used the seasonal dynamics data. Each individual matrix was a table where rows and columns represented species and months respectively. Table entries were the average number of individuals collected for each species at a given month. (2) Niche partitioning according to species vertical distribution is a common feature in soil animal communities (Lavelle & Spain 2001, Wardle 2002). When foraging at different depths, earthworm species may reduce competition by feeding on different types of organic resources (Bouché 1977). Vertical niche partitioning among Carimagua's earthworms has been suggested by Jiménez & Decaëns (2000), who found that the average living depth differed substantially among species. To quantify and test vertical niche overlap, we used individual matrices in which rows and columns represented species and soil strata, respectively, and where entries consisted of the mean number of individuals collected in each stratum over the total study period. As most species were not represented below 40 cm, we performed the analysis with the data of the first three 10-cm layers, and bulked the deeper layers into a single '<30 cm' category. (3) In ecological communities, ecologically similar species that are also morphologically alike might not co-exist because of excessive overlap in their resource uses (Hutchinson 1959). Consequently, biometric traits have been widely used to quantify the influence of competition on community assembly (Dayan & Simberloff 2005). Biometric niche overlap was calculated for individual matrices where rows and columns represented species and biometric traits, respectively, and where the entries consisted of the mean trait values measured for the collected individuals. Here, we used three traits (body length, weight and preclitellar diameter) that describe earthworm external morphology in a reliable way (Jiménez 1999). To avoid any influence of the measurement units in the index calculation, data were previously standardized by dividing each value by the standard deviation of the corresponding column in the matrix.

Mean niche overlap was calculated for each patch- and plot-level assemblage and compared with a null model in which the observed data were randomized among species (10 000 iterations). If competitively structured, a given assemblage should present less niche overlap than EBC for the dimensions of the niche that are subject to competition. We used a randomization algorithm that retains the niche breadth of each species, but randomizes

which particular resource states are utilized (RA3 in Albrecht & Gotelli 2001). It corresponds to a simple reshuffling of each row of the matrix that assumes all the different resource states to be equally abundant (or usable) by all species. Calculations and tests were done with the 'Niche Overlap' module of Ecosim.

Size distribution analysis

We tested if identified assemblages presented patterns that limit biometric similarity between co-existing species for the three morphometric traits that were used in the niche overlap analysis. For each trait, we calculated: (1) the minimum segment length (MSL), which is the smallest size difference found in all available pairs of species; (2) the variance in segment length (VarSL) that measures the overall tendency for the trait values to be evenly spaced. Both metrics were successively computed after log-transforming the data, which allowed analysing the size ratio of the considered trait (Gotelli & Ellison 2002). Observed values were calculated for all assemblages that comprised more than two species, and were compared with those obtained for 10 000 random assemblages. In a competitively structured community or assemblage, MSL and VarSL should be higher and lower than EBC, respectively (Gotelli & Ellison 2002). We used a null model algorithm which takes the largest and smallest species in the assemblage to set the minimum and maximum boundaries for the simulation. The remaining (n − 2) species were chosen from a random, uniform distribution within these limits. This null model assumes that in evolutionary time, any possible configuration of body sizes is equiprobable within the limits imposed by the largest and smallest species (Gotelli & Ellison 2002). Calculations and tests were done with the 'Size Overlap' module of Ecosim.

Data comparisons

For each index (Pianka's and Czechanowski O_{ik}, MSL, VarSL), we calculated the standardised effect size (SES):

$$SES = \frac{(I_{obs} - I_{sim})}{S_{sim}}$$

where I_{sim} is the mean index of the simulated assemblages, S_{sim} is the standard deviation, and I_{obs} is the observed index (Gotelli & Graves 1996). For each type of assemblage (patch-level or plot-level) and each index, we further calculated the average values of the observed and simulated indices, and the average corresponding SES.

We used a permutation test to compare: (1) the average values of the observed indices with those of simulated assemblages; (2) the average observed values obtained in patch-level assemblages with those obtained for plot-level assemblages. A similar approach was used to test whether average SES values obtained for a given set of assemblages did differ from zero or not. Each test involved 10 000 iterations in which the data were reshuffled among the categories to determine how much variation was expected among the means. The null hypothesis was that the observed variation among the means of the groups was no greater than EBC. Calculations were performed using the 'Anova' module of Ecosim.

RESULTS

Earthworm assemblage composition

A total of six species, all still undescribed and all native from the study region, was identified in the six sampled plots (Jiménez 1999). Apart from *Andiorrhinus* sp., which occurred only in Pasture 1 and Savanna 1, all species were present in all the plots (Tables 1 and 2). Mean total earthworm density and biomass respectively ranged from 16–25 ind. m^{-2} and 1.7–4.2 g fw m^{-2} in the savannas, and 45–97 ind. m^{-2} and 5.5–62.1 g fw m^{-2} in the pastures. Detailed studies of species assemblage composition in the different study plots have been published previously in Decaëns & Jiménez (2002) and Jiménez *et al.* (1998b). The highest densities were recorded for *Glossodrilus* sp. and, in the pastures, Ocnerodrilidae sp. Depending on the

Table 1. Main features of the spatio-temporal distribution of earthworm communities in the six study plots as described by the partial triadic analyses. CPI1 = first axis of the interstructure analysis; CPC1 = first axis of the compromise analysis; Moran's P = significance level of the spatial patterns.

Plots	Number of species	% inertia CPI1	% inertia CPC1	CPC1 patch range (metres)	CPC1 Moran's P
Pasture 1	6	44.9	28.1	22.0	< 0.001
Pasture 2	5	20.2	34.2	22.4	< 0.001
Pasture 3	5	17.9	35.3	11.2	0.003
Savanna 1	6	38.4	33.1	33.0	< 0.001
Savanna 2	5	14.6	36.4	11.9	< 0.001
Savanna 3	5	12.9	36.6	6.0	0.002

Table 2. Composition of the species assemblages in the six study plots. For a given plot, species with the same letters belong to the same patch-level assemblage as identified by the first component of the compromise analysis (a = species with positive scores; b = species with negative scores). Species codes: And = *Andiodrilus* sp.; Anr = *Andiorrhinus* sp.; Aym = *Aymara* sp.; Glo = *Glossodrilus* sp.; Mar = *Martiodrilus* sp.; Ocn = Ocnerodrilidae.

	Ocn	Mar	Glo	And	Aym	Anr
Pasture 1	a	b	a	b	b	a
Pasture 2	a	a	a	b	b	–
Pasture 3	b	b	a	a	b	–
Savanna 1	b	b	a	b	b	a
Savanna 2	a	b	b	a	a	–
Savanna 3	a	a	b	b	b	–

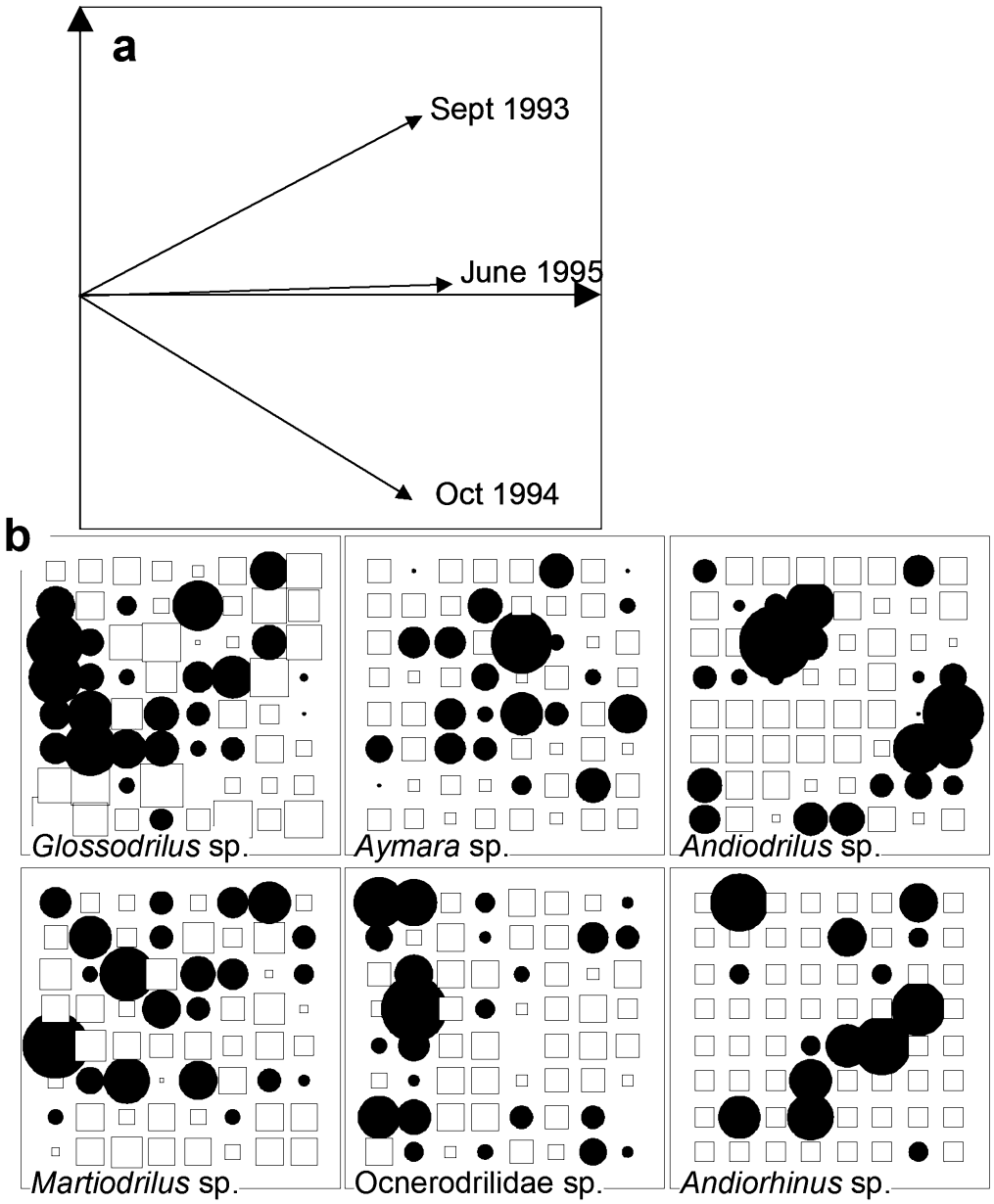

Figure 1. Interstructure analysis of the species assemblage structure in pasture 1: ordination of sampling dates on the plan defined by the first two axes of the PCA on the interstructure matrix (a); maps of the factorial coordinates of the 64 sampling points on the first axis of the interstructure analysis for each of the six species identified in the pasture (b) (circles and squares represent positive and negative scores and the size is proportional to the corresponding value). Modified from Figure 1 in Jiménez *et al.* (2006) *Acta Oecologica* 30: 299–311. Copyright © by Elsevier. Reprinted with permission of the publisher.

plot, the highest contributions to biomass were recorded for *Glossodrilus* sp., *Andiodrilus* sp. or *Martiodrilus* sp., the latter being dominant in the three pastures.

Earthworm assemblage spatial patterns

The percentages of the total inertia explained by the first axes of the PTA's interstructure and compromise analyses are presented in Table 1. Values were always lower than 50%, indicating relatively little inertia in the data. Interstructure analyses described the patterns of population distribution that were stable across time. Most species were significantly aggregated, but high-density patches had sharper boundaries for endogeic species (e.g. *Glossodrilus* sp., *Andiodrilus* sp.), and were more diffuse for surface-dwelling species (*Aymara* sp. and *Martiodrilus* sp.) (Figure 1). Compromise analyses described the species assemblage patterns that were stable across time, and highlighted clusters of species

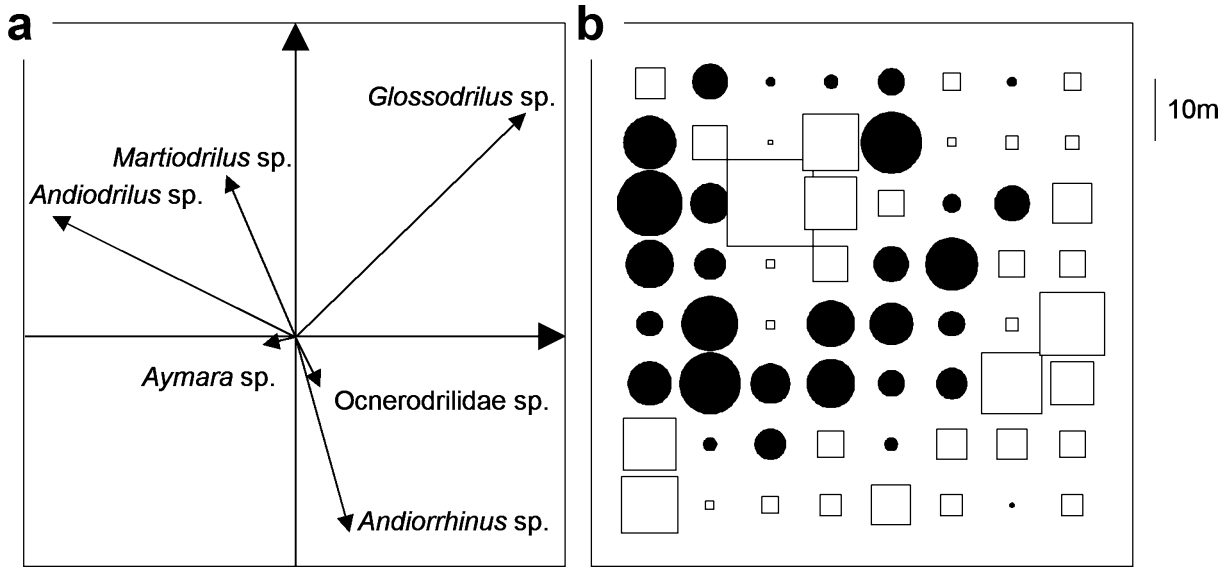

Figure 2. Compromise analysis of the species assemblage structure in pasture 1: correlation circle showing the ordination of the variables (species) on the factorial plan defined by the first two axes of the PCA on the compromise matrix (a); maps of the factorial coordinates of the 64 sampling points on the first axis of the PCA on the compromise matrix (b) (circles and squares represent positive and negative scores respectively and the size is proportional to the corresponding value). Modified from Figure 2 in Jiménez *et al.* (2006) *Acta Oecologica* 30: 299–311. Copyright © by Elsevier. Reprinted with permission of the publisher.

that shared similar spatio-temporal distributions (similar relative position on the first axis) (Figure 2, Table 2). According to Moran's autocorrelograms, sample scores on the first compromise axis were significantly aggregated in space over ranges of 6 to 33 m (Table 1). In each sampled plot, earthworm assemblages thus presented non-random and statistically significant spatio-temporal structure consisting in a juxtaposition of patches characterized by dominant 'patch-level assemblages'. As an example, the compromise analysis of Pasture 1 distinguished ($P < 0.001$, Table 2) a cluster composed of *Martiodrilus* sp., *Andiodrilus* sp. and *Aymara* sp. from another with *Glossodrilus* sp., *Andiorrhinus* sp. and Ocnerodrilidae sp. (Figure 2). The six PTAs thus identified 12 patch-level assemblages (Table 2) differentiated within the six plot-level assemblages (i.e. the complete species list occurring in a given plot).

Niche overlap patterns

Both the Pianka and Czechanowski indices provided very similar results and we thus decided to present only those obtained with the former. Temporal niche overlap was significantly higher than EBC for the majority of patch- and plot-level assemblages (Table 3) and average observed overlaps were unusually high ($P = 0.050$ and $P = 0.002$, respectively). Average SES was significantly higher than 0 at both scales, but was significantly lower in patch- as compared with plot-level assemblages (Table 3).

Table 3. Results of the niche overlap analysis. For each niche axis, we analysed niche overlap patterns for both patch-level assemblages (species with same signs on the first compromise axis, but see Table 2) and plot-assemblages (species present in a given plot). 'Lower tail' and 'Upper tail' indicate the number of assemblages for which the observed Pianka O_{ik} was respectively less than or greater than predicted by the null model. The number in parentheses indicates the number of assemblages with significant patterns ($P < 0.05$, one-tailed test). Different letters indicate significant differences between observed and EBC averages ($P < 0.05$, one-way ANOVA). The P values indicate the probability of accepting the null hypothesis that the standardized effect size (SES) differed from zero, and the P* values the probability of having no significant difference between SES calculated for patch-level and plot-assemblages (one-way ANOVA).

Niche dimension	Assemblage	Lower tail	Upper tail	Average obs. Pianka's O_{ik}	Average EBC Pianka's O_{ik}	Average SES	P	P*
Vertical	Patch	4(0)	8(4)	0.70a	0.49b	0.81	0.01	0.24
Vertical	Plot	0(0)	6(3)	0.62a	0.51b	1.48	0.00	
Seasonal	Patch	2(2)	10(7)	0.75a	0.63b	1.35	0.03	0.02
Seasonal	Plot	0(0)	6(6)	0.75a	0.63b	3.65	0.002	
Biometric	Patch	9(1)	3(0)	0.71a	0.75a	–0.38	0.18	0.53
Biometric	Plot	3(0)	3(0)	0.80a	0.80a	–0.07	0.73	

Table 4. Results of body-size structure analysis. For each biometric trait, we analysed minimum segment length (MSL) and its variance (VarSL) for both patch-level assemblages and plot-assemblages. 'Lower tail' and 'Upper tail' indicate the number of assemblages for which the observed metric was respectively less than or greater than predicted by the null model. The number in parentheses indicates the number of assemblages with significant patterns ($P < 0.05$, one-tailed test). Different letters indicate significant differences between observed and expected by chance (EBC) averages ($P < 0.05$, one-way ANOVA). The P values indicate the probability of accepting the null hypothesis that the standardized effect size (SES) differed from zero, and the P* value the probability of having no significant difference between SES calculated for patch- and plot-assemblages ($P < 0.05$, one-way ANOVA).

Biometric trait	Metric	Assemblage	Lower tail	Upper tail	Average obs. metric	Average EBC metric	Average SES	P	P*
Length	MSL	Patch	1(0)	6(2)	0.26a	0.15b	0.91	0.02	0.02
Length	MSL	Plot	5(0)	1(0)	0.04a	0.05a	−0.07	0.77	
Length	VarSL	Patch	6(2)	1(0)	0.02b	0.06a	−0.43	0.02	0.82
Length	VarSL	Plot	6(0)	0(0)	0.02b	0.03a	−0.39	0.00	
Weight	MSL	Patch	1(0)	6(0)	1.17a	0.90a	0.40	0.01	0.86
Weight	MSL	Plot	2(0)	4(1)	0.24a	0.19a	0.47	0.16	
Weight	VarSL	Patch	6(0)	1(0)	0.17b	1.05a	−0.43	0.002	0.62
Weight	VarSL	Plot	6(0)	0(0)	0.20b	0.40a	−0.50	0.002	
Diameter	MSL	Patch	1(0)	6(1)	0.28a	0.18b	0.70	0.06	0.02
Diameter	MSL	Plot	5(0)	1(0)	0.04b	0.06a	−0.31	0.02	
Diameter	VarSL	Patch	6(1)	1(0)	0.05a	0.10a	−0.31	0.08	0.55
Diameter	VarSL	Plot	6(0)	0(0)	0.02b	0.05a	−0.46	0.001	

At both patch- and plot-levels, vertical niche overlap was almost always significantly higher than EBC, average observed Pianka's O_{jk} was higher than mean simulated value ($P = 0.018$ and $P = 0.001$, respectively), and the average SES was significantly higher than 0 (Table 3). Average SES was not significantly different between patch- and plot-level assemblages.

Biometric niche overlap was lower than EBC in a majority of patch assemblages, but the observed and EBC values were not significantly different, and the SES was not significantly lower than 0 (Table 3). Patterns were mainly random for plot-level assemblages and no significant difference was found when comparing average SES calculated for patch- and plot-level assemblages.

Size distribution patterns

Patch-level assemblages showed a consistent trend toward over and even spacing of body length (Table 4). MSL was higher than EBC in six of seven cases (with significant individual tests in two of them), average MSL tended to be higher than EBC ($P = 0.026$) and had a SES significantly higher than 0. Conversely, plot-level assemblages were characterized by random body length ratio patterns and, when compared with patch-level assemblages, lower average value of the SES calculated for MSL. The VarSL was lower than EBC in the majority of patch and plot assemblages (with two individually significant values for patch-level assemblages), showed an unusually small average ($P = 0.011$ for both patch- and plot-level assemblages), and a SES significantly lower than 0.

Body weight tended to be over spaced in both patch- and plot-level assemblages (Table 4): although average observed values were not significantly higher than simulated ones, the corresponding SESs were significantly higher than 0. Average VarSL was also less than EBC ($P = 0.001$ and $P = 0.009$ for the patch- and plot-levels, respectively), with a SES lower than 0. These patterns should however be viewed with caution, as they were weakly supported by individual matrix analyses which on the whole did not differ from the null model (no significant individual test found for VarSL, and only a single instance found for MSL in Savanna 1). Differences among SES calculated at the patch and at the plot scales were not significant.

Size analysis of body diameter provided results similar with the analysis of body length (Table 4). In patch-level assemblages MSL was higher than EBC in six of seven cases (with significant individual tests in one of them), average MSL was significantly higher than EBC ($P = 0.050$) and SES was significantly higher than 0. An opposite trend was found in plot-level assemblages, where mean MSL was lower than EBC ($P = 0.025$), with an average SES significantly lower than 0 and lower than the SES calculated for patch-level assemblages. Although only a single significant individual value was detected, the VarSL was lower than EBC in nearly all of the patch and plot assemblages. For plot-level assemblages, the mean VarSL was significantly lower than expected by chance ($P = 0.001$), and the corresponding average SES was lower than 0. A similar, although not significant, pattern was found for patch-level assemblages.

DISCUSSION

The spatial organization of earthworm assemblages in alternating patches characterized by specific species

assemblages has been found in both tropical and temperate soils (Margerie *et al.* 2001, Nuutinen *et al.* 1998, Poier & Richter 1992, Rossi 2003). Except for savanna 1, the spatial extent of the patches found in our study (6–22 m) was in the lower range of what is reported in other studies (20–50 m) (Margerie *et al.* 2001, Rossi 2003). This may be because assemblages were dominated by small and weakly mobile species (*Glossodrilus* sp., Ocnerodrilidae sp. and *Andiodrilus* sp.) that aggregate at small spatial ranges (Decaëns & Rossi 2001, Jiménez *et al.* 2001, 2006a). The spatial range of patches is thus likely to be context dependent, and aggregation at larger scales is often observed in assemblages with a higher contribution of large and more vagile species, such as in European grasslands (Margerie *et al.* 2001) or African savannas (Rossi 2003).

The structured proportion of the spatio-temporal variability in earthworm assemblages remained low as indicated by the percentage of inertia associated with the first axes of both the interstructure and compromise analyses. This indicates a high residual variability from the analysis, which may result from different sources including species vagility (Decaëns & Rossi 2001), sampling error (Jiménez *et al.* 2006b) and/or small-scale variability (below the minimum inter-sample distance) in species distribution (Rossi & Nuutinen 2004). All these factors are likely to differ substantially among species, and thus to increase the residual noise in the data matrices. However, despite this residual variability, we observed non-random and statistically significant patterns in the six studied plots. This consistency suggests that the spatio-temporal arrangements of species assemblages are generated by deterministic assembly rules rather than by random events.

The reason why patch-level assemblages differed so much in composition among plots of the same habitat type is an interesting question that will require additional information to be elucidated. Differences between species assemblages of apparently similar habitats might be due to slight environmental differences that may confer a slight selective advantage to colonists of particular species (Diamond 1975). In our case, however, the detailed study of the sampled plots provided no evidence that this mechanism may account for the observed differences in assemblage composition (Decaëns & Rossi 2001, Jiménez *et al.* 2001, 2006a). Alternatively, chance in the form of random historical events (e.g. chronological order in colonization events) might play a large role in building up non-identical assemblages that represent stable equilibria (Diamond 1975). Any given patch-assemblage would thus represent one of many possible, alternative, stable assemblages that could be constructed on paper from the same species pool.

Despite the widely accepted idea that earthworm species show a high degree of niche partitioning with regards to vertical distribution (Bouché 1977, Lavelle & Spain 2001), we reported a niche overlap according to this dimension higher than EBC. This is an unexpected result, as the local pool comprises species of different ecological guilds that are supposed to differ substantially in their yearly average vertical distribution. Similarly, we found a higher seasonal niche overlap than EBC, in accordance with the review of Schoener (1974) who concluded that animals often segregate along food and habitat dimensions but rarely along temporal niche axes. These results suggest strong constraints on membership in assemblages (Weiher & Keddy 1995). Ecological theory predicts that environmental conditions acting as strong habitat filters may induce an underdispersion of the traits associated with these pressures (Keddy 1992, Keddy & Weiher 1999, Weiher & Keddy 1995). The low levels of organic matter, its concentration in the superficial soil layers and the high seasonality of rainfall may for example select earthworm species that display dormancy during the dry season, concentrate their activities during the rainy period and/or locate their foraging activities in the first 20 cm of the soil profile (Jiménez & Decaëns 2000, Jiménez *et al.* 2000). Alternatively, niche overlap SES were on average significantly lower in patches than in plot-assemblages, which suggests that competition is reduced in patches by limiting ecological similarity between species that co-exist at this scale.

The idea that co-existing species should differ in morphology in order to reduce resource use overlap is supported by a great amount of empirical evidence (Dayan & Simberloff 2005, Weiher & Keddy 1995). For instance, patterns of limiting similarity, such as ecological and community-wide character displacements, have been reported for many groups of vertebrates but more rarely for invertebrates (see review by Dayan & Simberloff 2005). Regular spacing of body size and morphometric overdispersion was however reported in assemblages of molluscs (Barker & Mayhill 1999, Chiba 2004, Grudemo & Johannesson 1999), crustaceans (Marchinko *et al.* 2004), beetles (Brandl & Topp 1985, Satoh *et al.* 2003, Sota *et al.* 2000), and ants (Gotelli & Ellison 2002, Nipperess & Beattie 2004). The only case study dealing with earthworms, an example of ecological character displacement in sympatry between congeneric species in Mexico (Fragoso & Rojas 1997), suggests that body shape is directly related to resource utilization. The relationship between species biometric features and life history strategies, and in particular resource uses, is also central in most eco-morphological classifications that are classically recognized in earthworm studies (Bouché 1977, Lavelle 1997). Despite the non-significance of the results obtained for biometric niche overlap, our data support this idea by demonstrating that a minimum level of morphometric differentiation in body sizes is necessary to allow species to co-exist in a given patch-level assemblage.

Competition may however generate different patterns according to the spatial scale considered. We found that body weight was significantly overdispersed and constant among species at both the plot and patch scales, while body length shows a similar pattern at the patch scale only. This suggests that both attributes may be directly related to different features of species feeding habits. Body weight is, for example, known to reflect the quality of the resource ingested by geophagous species (Lavelle 1981): small species are often specialized for organic-rich substrates (e.g. litter, root exudates, vertebrate faeces, etc.), while larger ones usually ingest a variable proportion of soil with lower organic content. Although litter-feeding species may not fully match this model, most earthworms of Carimagua were described to feed at least partly on soil (Jiménez *et al.* 1998b, Mariani *et al.* 2001), and different weights among species may thus reflect differences in the organic content of their food substrate. Alternatively, species body length was reported to reflect the size of the ingested soil particles, although no general pathway for this relationship has been pointed to date (Blanchart *et al.* 1997, Lowe & Butt 2003). Differentiation of trophic niches according to both the organic content and particle size of the ingested material among earthworm species has been reported in a number of other studies (Curry & Schmidt 2007). Our results thus suggest that species may co-exist in a given plot thanks to a minimum level of niche partitioning with regards to the organic content of their feeding substrate. At a lower scale, assemblage patchiness would result from spatial segregation between species competing for similar particle size classes, and from within-patch complementarity between species of different body size. This last hypothesis was first proposed by Rossi (2003) for earthworm assemblages of savanna soils of Côte d'Ivoire, and is supported in our results by some conspicuous trends in pairwise relationships among species. For example, the large-sized *Martiodrilus* sp. is associated in four of six cases with the small Ocnerodrilidae sp., which feeds upon the large casts produced by the former species (Jiménez *et al.* 2006a). Conversely, *Andiodrilus* sp. and *Glossodrilus* sp., two potentially competing geophagous species with relatively similar biometric features, are segregated in different patches in four cases of six (Table 2). Although these patterns of coexistence/segregation are not strong, it is reasonable to interpret them as being consistent with the overall conclusion that the spatial structure of earthworm assemblages is non-random and mainly reflects competition versus complementarity interactions between species.

Our results broadly demonstrate that competition influences assemblage structure more strongly within patches than within plots, and therefore plays a significant role in the spatial patterning of earthworm assemblages below the plot scale. This supports the conclusions of a recent study that pointed to competition as the main assembly constraint in earthworm assemblages of north-western France (Decaëns *et al.* 2008). The exact mechanisms involved in earthworm interspecific interactions are however still poorly known. Dalby *et al.* (1998) found that competition among species may result from direct cocoon consumption. Such intra-guild predation has been reported for a number of other animals, e.g. birds (Hakkarainen & Korpimaeki 1996, Spooner *et al.* 1996), fish (Garner 1996), salamanders (Roudebush & Taylor 1987) and scorpions (Polis & McCormick 1987). It is assumed to increase the competitiveness of the predating competitor through an enhanced nitrogen intake (Matsumura *et al.* 2004). Additionally, earthworms are ecosystem engineers (sensu Jones *et al.* 1994) able to physically modify their environment, thus altering resource availability for other species. Soil engineering has been reported as a possible mechanism of interspecific competition among earthworm species or between earthworms and other groups of organisms. As an example, deep-burrowing species may deprive surface-dwellers of their habitat and trophic substrate when actively burying litter into the soil (Dalby *et al.* 1998, Hendrix *et al.* 2006). Geophagous species may also interact, either positively or negatively, with each other by modifying the size distribution of soil aggregates, and therefore their availability as a readily ingestible substrate for other species (Blanchart *et al.* 1997, Lowe & Butt 2003). As proposed by Hastings *et al.* (2007), more research should be undertaken to improve our comprehension and to quantify the role of earthworm engineering activities relative to other processes such as resource competition and trophic interactions.

In conclusion, our study supports the model of Weiher & Keddy (1995) that species traits associated with meeting the challenges of competition adversity (morphometric traits) are overdispersed, while those associated with environmental pressure (vertical and temporal distribution) are underdispersed. The assembly rules that emerge from our results are: (1) at the plot scale, body weights of co-existing earthworm species show a significant trend toward overdispersion and low variance of segment length, seasonal and vertical niche overlap are higher than EBC and species are aggregated in discrete patches; (2) at the scale of these patches, niche overlap is reduced when compared with the plot scale, and body length and diameter of co-existing species are overdispersed and display low variance in segment length.

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